Functional aspects of metatarsal head shape in humans, apes, and Old World monkeys

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Dorsal doming

27

28 **Abstract**

29 Modern human metatarsal heads are typically described as “dorsally domed,”
30 mediolaterally wide, and dorsally flat. Despite the apparent functional importance of these
31 features in forefoot stability during bipedalism, the distinctiveness of this morphology has not
32 been quantitatively evaluated within a broad comparative framework. In order to use these
33 features to reconstruct fossil hominin locomotor behaviors with any confidence, their connection
34 to human bipedalism should be validated through a comparative analysis of other primates with
35 different locomotor behaviors and foot postures, including species with biomechanical demands
36 potentially similar to those of bipedalism (e.g., terrestrial digitigrady). This study explores shape
37 variation in the distal metatarsus among humans and other extant catarrhines using three-
38 dimensional geometric morphometrics (3DGM). Shape differences among species in metatarsal
39 head morphology are well captured by the first two principal components of Procrustes shape
40 coordinates, and these two components summarize most of the variance related to “dorsal
41 doming” and “dorsal expansion.” Multivariate statistical tests reveal significant differences
42 among clades in overall shape, and humans are reliably distinguishable from other species by
43 aspects of shape related to a greater degree of dorsal doming. Within quadrupeds, terrestrial
44 species also trend toward more domed metatarsal heads, but not to the extent seen in humans.
45 Certain aspects of distal metatarsus shape are likely related to habitual dorsiflexion of the
46 metatarsophalangeal joints, but the total morphological pattern seen in humans is distinct. These
47 comparative results indicate that this geometric morphometric approach is useful to characterize
48 the complexity of metatarsal head morphology and will help clarify its relationship with function
49 in fossil primates, including early hominins.

Introduction

The evolutionary transition of the hominin foot from a primitive grasping organ into a propulsive lever adapted for obligate terrestrial bipedality—a hallmark of human evolution—is a key focus of paleoanthropological research (Morton, 1922, 1924; Elftman and Manter, 1935; Wood-Jones, 1944; Bojsen-Møller, 1979; Lewis, 1980; Susman, 1983; Latimer et al., 1987; Richmond et al., 2001; Harcourt-Smith and Aiello, 2004; Jungers et al., 2009; Lovejoy et al., 2009; Pontzer et al., 2010). Researchers have proposed different mechanistic models for the evolutionary sequence of modifications that led to the derived human condition (e.g., Morton, 1964; Susman, 1983; Lewis, 1989; Kidd, 1999; DeSilva, 2010). However, the fragmentary fossil record and the mosaic nature of fossil hominin pedal morphologies complicates attempts to build a consensus model of hominin foot evolution despite the extensive literature on the topic (Stern and Susman, 1983; Latimer et al., 1987; Susman and Brain, 1988; Harcourt-Smith and Aiello, 2004; Susman and deRuiter, 2004; Zipfel and Kidd, 2006; Jungers et al., 2009, 2015; Zipfel et al., 2009, 2011; Pontzer et al., 2010; Ward et al., 2011, 2012; DeSilva et al., 2012; Haile-Selassie et al., 2012). What remains clear, however, is that modern human feet are well adapted for obligate bipedal locomotion. In combination, several derived features (e.g., an adducted, robust hallux; a midfoot stabilized by various soft tissues) enable the human foot to act efficiently as a stiff lever during the propulsive phases of bipedal gait (Elftman and Manter, 1935; Hicks, 1954; Morton, 1964; Lewis, 1980; Gomberg, 1985; Sarrafian, 1987; Harcourt-Smith and Aiello, 2004; but see Bates et al., 2013; DeSilva and Gill, 2013; DeSilva et al., 2015). These derived features presumably evolved as a consequence of selective pressures acting on the hominin foot during its transition from a primitive grasping organ used in arboreal locomotion (Stern and Susman, 1983; Susman et al., 1984; Stern, 2000; Lovejoy et al., 2009; but see Ward, 2002) to one used during

habitual terrestrial bipedalism (Susman and Stern, 1982; Spoor et al., 1994; Ruff, 2008, 2009; Pontzer et al., 2010).

The forefoot is a functionally important region that includes the metatarsophalangeal joints (MTPJs). A more dorsally projecting metatarsal (MT) head is thought to increase the dorsiflexion range of motion (ROM) at the MTPJs (Ward et al., 2011; DeSilva et al., 2012). This increased ROM serves to stabilize the forefoot and aids propulsion at the end of stance phase by tightening the plantar aponeurosis, which is a fibrous band that originates from the calcaneal tuberosity and inserts distally on the proximal phalanges (DeSilva, 2010; Griffin et al., 2014). This tightening of the plantar aponeurosis has been likened to a “windlass mechanism” (Hicks, 1954; Bojsen-Møller, 1979; Susman, 1983; Griffin and Richmond, 2010; Griffin et al., 2014) wherein it is analogous to a cable, the metatarsal head a drum, and the proximal phalangeal base a handle. During toe-off, the plantar aponeurosis becomes taut and the medial longitudinal arch of the foot is raised. This changes the conformation of the midfoot into a more rigid lever that improves propulsion and stability during bipedalism. Conversely, a more plantarly oriented MT head is hypothesized to increase plantar flexion ROM for arboreal pedal grasping (Stern and Susman, 1983; Hamrick, 1996); this plantar orientation likely impedes the mechanical advantage of the windlass mechanism, resulting in reduced dorsiflexion at toe-off (Griffin et al., 2010b; Holowka et al., 2014). However, additional factors such as digit length may also reduce toe-off dorsiflexion in the hominoid because the longer toes of the hominoids would be subject to greater bending stresses while dorsiflexed compared to the shorter toes of modern humans (Preuschoft, 1970; Tuttle, 1970).

In addition to MT head projection, other researchers have emphasized a flattened mediolateral expansion of the dorsal aspect of the MT head as necessary for joint stability under

increased loads during modern human-like toe-off (Susman and Brain, 1988; Susman and deRuiter, 2004; Pontzer et al. 2010). Wide and flat MT heads in humans are easily distinguished qualitatively from the narrow, rounded condition seen in *Pan* and other primates (Fig. 1). Dorsal mediolateral expansion of the MT head allows for “close-packing” of the MTPJs by tightening the collateral MTP ligaments in the dorsiflexed configuration. In the close-packed position, the contact surface of the MT head and proximal phalangeal base articular surfaces is maximized and tightening of collateral ligaments limits joint motion in other anatomical planes when the MTPJs are dorsiflexed, thus increasing joint stability when maximum joint congruency is achieved (MacConaill and Basmajian, 1969; Stern and Susman, 1983; Susman et al., 1984; Susman and Brain, 1988; Susman and deRuiter, 2004). This same mechanism is hypothesized to close-pack the ape MTPJs in plantar flexion for increased stability during pedal grasping (Susman, 1983).

Detailed morphometric analyses have been conducted on the proximal MT articular surface (Proctor et al., 2008; Proctor, 2010a, b, 2013), and a few quantitative approaches to distal MT and proximal phalangeal functional morphology (e.g., Duncan et al., 1994; Griffin et al., 2010a; Congdon et al., 2011) have been investigated as well. MT head “dorsal doming” has been qualitatively described in fossil hominins extensively (Stern and Susman, 1983; Susman and Brain, 1988; Susman and deRuiter, 2004; Jungers et al., 2009; Lovejoy et al., 2009; Ward et al., 2011; DeSilva et al., 2012; Haile-Selassie et al., 2012), but quantitative data on distal MT surface morphology relating to “dorsal doming” is lacking, therefore precluding morphometric comparisons of this phenomenon. The current lack of quantitative data makes it difficult to ascertain more precisely the functional importance of hypothesized bipedal specializations, especially when these complex morphologies are combined and simplified into a binary

character state (e.g., domed versus not domed). Additionally, although modern humans qualitatively possess dorsally oriented and dorsally flat, wide MT heads, many fossil hominins lack one or more of these “defining bipedal features” (Susman and deRuiter, 2004; Lordkipanidze et al., 2007; Pontzer et al., 2010; DeSilva et al., 2012).

The goal of this study is to quantify “dorsal doming” in all five MTs within an extant comparative context. Dorsal MT head orientation, mediolateral dorsal expansion of the MT head, and dorsal overlap of the MT head onto the diaphysis are often considered signature features of human bipedality. However, we hypothesize that some of these characters might reflect signals of terrestriality more generally for other taxa that stereotypically dorsiflex their forefoot joints during quadrupedal locomotion. For example, different foot postures (e.g., plantigrade versus digitigrade), substrate use (e.g., terrestrial versus arboreal), and even speed of travel can also influence habitual MTPJ ROM during locomotion (Meldrum, 1991; Hayama, 1994; Schmitt and Larson, 1995; Vereecke et al., 2003; Nowak et al., 2010; see also Patel, 2010a and Patel and Polk, 2010 for analogous data in the MCPJs). If dorsal orientation of the MT head facilitates greater potential for dorsiflexion at the MTPJs (Susman, 1983; Stern and Susman, 1983; Susman and deRuiter, 2004; Ward et al., 2011, 2012 DeSilva et al., 2012), we expect to see at least some evidence of dorsal MT head orientation in digitigrade, more habitually terrestrial genera such as *Papio* (Meldrum, 1991; Schmitt and Larson, 1995; but see Patel, 2010b). Therefore, we predict that humans will still be unique in consistently demonstrating all of these derived morphologies simultaneously, but we also suspect that more terrestrial and more digitigrade taxa will show some degree of convergence with humans. In contrast, we predict that habitually arboreal quadrupeds and suspensory species should have more plantarly oriented metatarsal heads than their more terrestrial counterparts. Although African apes are more terrestrial than Asian apes

(Doran, 1992, 1993, 1996; Fleagle, 2013), they also exhibit pedal grasping adaptations for vertical climbing of large supports and frequently engage in suspension (Tuttle, 1970; Bojsen-Møller, 1979; Lewis, 1980; DeSilva, 2008, 2009). Moreover, African apes do not greatly dorsiflex their toes during the push-off phase of knuckle-walking quadrupedalism (Griffin et al., 2010b; Holowka et al., 2014); accordingly, despite their typical use of terrestrial locomotion during travel, we predict that African apes will demonstrate little to no dorsal doming.

Materials and Methods

This study quantifies shape differences in distal metatarsals 1–5 within a comparative sample of 540 metatarsals drawn from 10 catarrhine species, with a sample size of at least 10 metatarsals per ray for all genera studied (Table 1). Specimens were sampled from the American Museum of Natural History (AMNH), the Smithsonian’s National Museum of Natural History (NMNH), the Academy of Natural Sciences of Philadelphia (ANSP), the Museum of Comparative Zoology at Harvard University (MCZ), and the Stony Brook University Museum (SBU). Distal metatarsal morphology was explored using 3D digital polygon models reconstructed from scan data collected via different methods including computed tomography (CT), micro-computed tomography (μ CT), and laser scanning (LS). Measurement error due to data acquisition method is known to be insignificant (Tocheri et al., 2011), so all imaging data were pooled. The great ape (e.g., *Pongo*, *Pan*, *Gorilla*) metatarsals were laser scanned using a NextEngine 3D laser scanner using a resolution of 10,000 points per square inch; 12 scans were taken at different positions and then merged using ScanStudio HD PRO software. Some specimens were CT scanned using a General Electric Lightspeed VCT CT scanner (120 kV, 250

mA, 1 mm slice thickness, 0.187 mm reconstruction increment, bone plus reconstruction) at Health Sciences Center, Stony Brook University. For others, μ CT scanning was done using a ScanscoMedical Viva CT 75 scanner and an isometric voxel scan resolution of 40–80 μ m, depending on the size of the specimen. 3D models from CT scans were constructed from DICOM data using Amira 5.3.3 software (Visage Imaging, Inc.). Scanning artifacts or anomalies in the polygonal mesh were corrected using Geomagic Studio 2012 SR1 (3D Systems, Inc) and MeshLab 1.3.2 (Visual Computing Lab—ISTI—CNR) software packages. All data were collected from right metatarsals whenever possible; however, left metatarsals were mirrored in Geomagic when right elements were unavailable.

The 3D shape of all five metatarsal heads were evaluated using a landmark based approach. A 5x5 3D surface patch of nine user-defined landmarks and 16 semi-landmarks was applied using *Landmark Editor* (Wiley et al., 2005) following the methods detailed in Alméjida et al. (2015). Landmarks were selected based on repeatability and the ability to capture the full surface morphology of the metatarsal head. The surface patch was bounded mediolaterally by the proximal termination of the distal epicondyles, dorsally at the proximal termination of the distal articular surface, and plantarly at the proximal termination of the plantar condyles (Fig. 2). Table 2 lists the specific anatomical locations of each landmark.

An analysis of measurement error to assess experimental repeatability for this study was conducted using methods described in Proctor (2010a). Single *Homo* MT1, *Papio* MT2, *Gorilla* MT3, *Pongo* MT4, and *Hylobates* MT5 specimens were selected at random and measured five times across separate days in order to assess intra-observer error. These genera were chosen as they represent a wide range of locomotor modes, body sizes, and phylogenetic affinities. The landmarks for each repeated measure were combined with their respective taxonomic sample and

subjected to a PCA. Relative clustering of repeated measures is used to assess the repeatability of the methods used in this study, as has been done elsewhere (Lockwood et al., 2002; Proctor et al., 2008; Proctor, 2010a).

Semi-landmarks were slid using the minimized Procrustes distance criterion (Rohlf, 2010); similar results were obtained using minimized bending energy algorithms (Bookstein, 1997). The slid coordinates were then subjected to a generalized Procrustes analysis (GPA; Gower, 1975) and then principal component analysis (PCA) was used to summarize and explore the observed variation in metatarsal head shape. Articular surface wireframes and polygonal mesh warps were constructed to visualize shape changes. Significant differences in principal component (PC) scores between taxonomic groups were analyzed using multivariate analysis of variance (MANOVA); Tukey's HSD was used for pairwise post-hoc comparisons. All PCs explaining at least 5% of the total shape variance were subject to these analyses, but because the first two PCs captured essentially all of the relevant distal articular morphology, only the results from PC1 and PC2 are presented. Box-and-whisker plots are shown to visualize the variation between species in specific MT head morphologies. To explore the effect of size on shape, multivariate allometric correlations were investigated by regressing all PC scores on log-transformed centroid size (CS). Sliding, GPA, and PCA analyses were performed in the R package *Geomorph* (ver. 2.12; Adams et al., 2014); boxplots and all statistical tests were performed in R 3.02 base package. Wireframe construction and allometric regressions were performed in *MorphoJ* (ver. 1.06b; Klingenberg, 2011); mesh warps were made in *Landmark editor*.

Results

210

211 *Repeatability*

212 Results of the repeatability experiment are shown graphically (Fig. 3). *Hylobates* MT5
213 bones were among the smallest in the sample, but 3D models displayed enough resolution for
214 repeatable landmark placement. In each instance, repeated measures formed a distinct cloud in
215 the morphospace with relatively little variance. Overall, the results suggest that 3D landmark
216 placement was repeatable.

217

218 *PCA/MANOVA*

219 For all MTs, the first five PCs each accounted for > 5% of the variance in the data (Table
220 3). PCAs separated major clades as well as genera in all but one bivariate scatterplot of the PC
221 scores. The exception is in MT5, where all monkey genera overlapped in the morphospace, but
222 otherwise the general trend was the same, with clear separation of monkey, ape, and human taxa.
223 MANOVAs showed significant differences in shape variables (PCs) among taxa for all five
224 bones; post hoc tests further revealed significant differences between all of the groups in the
225 sample, but because the pattern seen in the lateral MTs was very similar, detailed tables are only
226 reported for MT1 and MT2 (Tables 4-7). Because PC1 and PC2 captured the relevant distal
227 articular surface morphology (see below), results for these two axes are reported in further detail.
228 For MT1, PC1 separated humans and all monkeys (*Nasalis*, *Macaca*, *Papio*) from the ape sample
229 ($p < 0.01$); apes generally overlapped with each other but *Pongo* was significantly different from
230 all groups ($p < 0.0001$) except *Gorilla*. In PC2, humans separated from cercopithecoids ($p <$
231 0.0001) and *Pan* ($p < 0.0001$). *Hylobates* had a large variance in PC2 and overlapped all groups

except *Homo* ($p < 0.0001$). Great apes generally overlapped on PC2, but *Pan* overlapped more with cercopithecoids than other apes and was significantly different from *Pongo* and *Gorilla* ($p < 0.0001$).

The pattern observed in the lateral MTs was very similar, but with some notable exceptions. Generally, more overlap in the morphospace was observed in the more lateral digits (MT4, MT5). PC1 separated humans from all taxa in MT5 ($p < 0.0001$), most taxa except *Pongo* and *Gorilla* in MT4 ($p < 0.0001$), cercopithecoids in MT3 ($p < 0.0001$), and *Pan* in MT2 ($p < 0.005$). In MT3, *Nasalis* formed a distinct cluster in the morphospace, separate from all groups on PC1 and intermediate between apes and papionins ($p < 0.0001$). PC2 separated humans from the rest of the extant sample in all lateral digits ($p < 0.0001$); humans were unique in PC2 in the lateral rays because the rest of the monkey and ape sample overlapped greatly in PC2 in all cases. Post hoc tests with locomotor mode as a fixed effect showed significant differences between broad locomotor repertoires (e.g., knuckle-walking versus arboreal quadrupedalism), but no significant differences between more similar locomotor repertoires such as arboreal versus semi-terrestrial quadrupedalism were observed.

Allometry

Multivariate allometric regressions of all PC scores on logCS were performed to explore correlations of shape and size across all MTs (Table 8). Size was not a significant correlate of shape in any MT. When controlling for phylogeny using phylogenetic independent contrasts (PICS; Felsenstein, 1985), the allometric regressions remain non-significant in all MT rays and the amount of variance explained by size drops dramatically in all cases. When a dummy code

for species was incorporated into the regression analyses, species became a consistently better predictor of shape than size for the lateral rays. Regressions were significant for MT2, MT3, and MT5 ($p < 0.05$). Overall these results suggest that MT size is not a strong determinant of MT shape, but rather that the shape differences observed are being driven by phylogenetic and functional differences.

Functional aspects of shape

Although the strength of the hypothesized functional signal varied among rays, PC1 and PC2 captured the same principal morphological differences in distal MT articular surface morphology across all rays. Moreover, PC1 and PC2 carry shape aspects that have been qualitatively related to bipedalism and other forms of locomotion and are therefore inspected in detail here. The pattern seen in the hallux was slightly different than in the lateral MTs. For MT1, PC1 (26% of variance) captured shape changes related to the overall dorsal versus plantar orientation of the MT head, as well as shape changes in plantar condylar morphology (Fig. 4). Positive PC1 scores indicate more dorsally oriented MT1 heads with a broader, shallower plantar condyle. Negative PC1 scores characterize more plantarly oriented MT1 heads with a deeply projecting plantar condyle flanked by steep, angular facets for articulation with the hallucal sesamoid bones. Box-and-whisker plots (Fig. 5) show that humans and monkeys overlap in PC1, and it is likely that this is driven more so by plantar condylar morphology than dorsal MT1 head orientation in most cases. Apes generally demonstrate much more plantarly oriented MT head morphology. PC2 (11% of variance) captured variance in the overall mediolateral breadth of the MT1 head. Low PC2 scores indicate greater mediolateral dorsal head width; monkeys and *Pan* are characterized by mediolaterally narrow heads, whereas *Pongo*, *Gorilla*, and humans have

277 more mediolaterally wide MT1 heads. Because PC2 tracked overall mediolateral MT head width,
278 PC1 and PC2 combined tracked dorsal mediolateral breadth in the MT1, which seems to be tied
279 to MT head orientation. Great apes and humans have wide MT1 heads, but great apes are wide
280 plantarly whereas humans are wide dorsally (Fig. 1).

281 For MT2–5, PC1 and PC2 explained nearly the same morphology and landmark
282 variation, differing only in the proportion of shape variance explained, and thus results for all
283 four metatarsals will be discussed together. PC1 (27–33% overall variance) captured two
284 principal shape changes: epicondylar breadth and dorsal versus plantar orientation of the MT
285 head relative to the epicondyles (Figs. 6 and 7). Higher PC1 scores describe a mediolaterally
286 wider and a somewhat more dorsally oriented MT head; lower PC1 scores describe a more
287 mediolaterally narrow and somewhat more plantarly oriented MT head. Apes have low PC1
288 scores for MT2–5 (Figs. 6 and 7); humans and monkeys have high PC1 scores. Monkeys
289 (especially *Papio*) have particularly high PC1 scores that are more driven by epicondylar breadth
290 than by dorsal orientation. The orientation of their MT heads is similar to the human condition,
291 both of which are more dorsally oriented than in apes.

292 PC2 (11–16% overall variance) captures dorsal mediolateral expansion/truncation of the
293 dorsal most part of the MT simultaneously with corresponding mediolateral truncation/expansion
294 of the plantar surface. Additionally, PC2 captures reduction in the medial and lateral
295 invaginations on the facet margins such that midway between the dorsal and plantar articular
296 surface margins, the mediolateral width of the facet increases with high PC2 scores. High PC2
297 scores indicate a more mediolaterally expanded dorsal MT head with corresponding plantar
298 surface truncation, as well as dorsal overlap of the articular surface onto the diaphysis (a
299 “domed” appearance). For all lateral MTs, humans form a distinct cluster in the morphospace

due to high PC2 scores; humans are distinct in the degree of mediolateral expansion of the dorsal MT head with wide mediolateral facet margins in the lateral rays. The entire range of the human sample does not overlap with any other sampled group (Fig. 7).

Discussion

Results from this study confirm that human MT head morphology can be distinguished quantitatively from that of other catarrhines in almost all cases. Importantly, this predicted result was more clearly demonstrated in the lateral MT data than in the hallux. This is a surprising result given the theorized importance of the hallux in human bipedalism. Although humans cluster well in the MT1 morphospace, the principal reason for the “noise” in the MT1 data is a slight overlap of modern human MT1s with the large bodied, highly arboreal colobine *Nasalis*. While the functional reason for this overlap is unclear, it is likely that this overlap is being driven primarily by shape information in PC1 relating to plantar condylar morphology. Many of the studied cercopithecoids have plantar condylar morphology similar to that of modern humans, both of which look different from extant great apes. Shape differences in plantar condylar morphology are particularly interesting because the fossil record has yielded multiple hominin and *Homo* MT1s demonstrating primitive, ape-like plantar condylar morphology such as SKX 5017 (Susman and Brain, 1988; Zipfel and Kidd, 2006), SK 1813 (Susman and deRuiter, 2004; Zipfel and Kidd, 2006), D2671 and D3442 (Lordkipanidze et al., 2007; Pontzer et al., 2010), and most recently KNM-ER-64062 (Jungers et al., 2015). It is possible that the shape differences observed in the plantar MT relate to the form of the hallucal sesamoid bones, whose shape may play a role in locomotor function (Le Minor, 1988). Further analyses of the plantar MT head and the hallucal sesamoids are needed to resolve these questions. In addition to primitive plantar

323 condylar morphology, these specimens all also have been described as having relatively
324 mediolaterally narrow dorsal MT heads compared to modern humans, which either challenges
325 the notion that a mediolaterally robust hallux is needed for human-like dorsiflexion during a
326 bipedal gait, or that these hominins walked with a rather different gait than do modern humans.
327 In short, if critical for human-like bipedalism, MT1 head widening and modern plantar condylar
328 morphology appears relatively late in the fossil record.

329 Humans are distinguished in lateral MTPJ anatomy by a total morphological pattern
330 typified by dorsally oriented, dorsally wide, and dorsally overlapped MT heads. This trait
331 complex probably reflects enhanced biomechanical function at the end of stance phase during
332 human bipedal gait (Susman and Brain, 1988; Susman and deRuiter, 2004; Griffin et al., 2010b;
333 Holowka et al., 2014). However, when functional characteristics of the lateral metatarsal heads
334 are mapped onto different principal components and analyzed separately, a somewhat more
335 nuanced pattern emerges. Humans and some other catarrhines overlap on PC1, which tracked
336 dorsal orientation of the MT head as well as epicondylar breadth. The overlap suggests that
337 dorsal orientation alone is not a bipedal adaptation per se, but rather an adaption more generally
338 to increased dorsiflexion angles experienced at the MTPJs related to foot postures and substrate
339 use. Although some cercopithecoids lie beyond humans on PC1, this is driven more by
340 epicondylar breadth than dorsal head orientation. We suspect that the particularly widely set
341 epicondyles of some cercopithecids (e.g., *Papio*) function to provide greater distance for the
342 collateral ligaments to tighten when stabilizing the MTPJs in the close-packed position of these
343 digitigrade/semi-digitigrade quadrupeds. This mechanism is similar to how the human MTPJs
344 must stabilize prior to toe-off during terrestrial bipedalism, and thus we suspect humans and
345 monkeys are overlapping in the same PC1 morphospace due to similar biomechanical demands

(e.g., high dorsiflexion ROM) placed on the foot during bipedalism and semi-terrestrial quadrupedalism. Our PC1 results suggest that plantar orientation of the MT head may be derived in apes relative to the ancestral condition, but stem hominoid fossils are needed in our analyses to confirm this possibility. Regardless, although PC1 separates humans from other apes, humans are not distinct in their lateral MT head orientation among other catarrhines. Unlike PC1, PC2, which tracked dorsal mediolateral MT head width, was the discriminating axis for humans with respect to the rest of the sample in the lateral MTs. This finding provides evidence for the importance of the lateral MTs in contributing to the propulsive advantage humans benefit from with the windlass mechanism at the MTPJs. Furthermore, it is likely that MTPJ joint stability is achieved by dorsal MT head widening (Susman and Brain, 1988; Susman and deRuiter, 2004), and this widening in the lateral MTs is a key morphological signal for inferring human-like forefoot mechanics and possibly locomotor behavior in the fossil record.

Conclusions

In this study, multivariate analyses of 3D shape data (3DGM) helped define and quantify dorsal doming as a functionally important forefoot adaptation for bipedalism. By exploring shape globally and in 3D, this quantitative study captured differences in MT head morphology without any subjective assumptions of what “dorsal doming” should look like. The multidimensional nature of the dataset allowed for a nuanced assessment of the distal metatarsus, identifying the major axes of metatarsal head shape variation as being related to dorso/plantar head orientation and mediolateral dorsal head breadth. These two shape changes, when present in concert better describe hominin forefoot adaptations. Importantly, dorsal doming is not a simple, binary morphology (domed versus not domed) limited to a distal MT surface projecting above the

diaphysis. The distinctive morphology seen in modern humans involves an overall dorsal orientation of the entire MT head combined with significant mediolateral expansion of the dorsal metatarsus and a dorsal articular surface overlap onto the diaphysis. These shape changes, captured in PC1 and PC2, yield a MT head shape that uniquely separates humans from the other catarrhines in our study. Our results also are consistent with the observations reported in the kinematic literature that show higher dorsiflexion angles at the MTPJs in humans compared to *Pan* (Griffin et al., 2010b, Holowka et al., 2014). Some of the morphological components that constitute “dorsal doming” are perhaps more generally related to habitual MTPJ dorsiflexion, but future analyses with fossils and ancestral state reconstructions are needed to further explore the evolution of MTPJ shape throughout primates. Still, the total morphological pattern observed within *Homo sapiens* offers a reasonably strong signal of modern human-like bipedalism and should serve as a useful benchmark for future analyses.

Future work should apply 3DGM methodology to fossil specimens as it appears robust and applicable to fragmentary specimens, and may provide finer resolution for fossils within an objective, functionally informative morphospace. Future quantitative studies should allow for a more nuanced interpretation of when—and in what combination—these features appear in the fossil hominin record. To inform discussions on evolutionary shape changes over time, the addition of fossil hominoid taxa (i.e., Miocene apes) is essential because adding these taxa will help calibrate ancestral state reconstructions revealing the polarity of shape changes (e.g., Almécija et al., 2013). Future studies with increased samples (per species) should also focus on locomotor differences between congeneric species (e.g., the more arboreal *Gorilla gorilla* versus the more terrestrial *Gorilla beringei*) to see if morphological differences in the distal MT correspond to observed differences in the positional behavior (e.g., Doran, 1996, 1997; Doran

and McNeilage, 1998) between these two species. There is a long standing and growing body of morphological literature that demonstrates significant anatomical differences between gorilla species (Schultz, 1930, 1934; Sarmiento, 1994; Harcourt-Smith, 2002; Tocheri et al., 2011; Dunn et al., 2014; Knigge et al., 2015), and an assessment of the distal metatarsus focused on gorilla species may lend additional support to this line of research. Finally, the distal half of the metatarsophalangeal joints—the proximal phalangeal base articular surface—should also be quantified using methods similar to those applied in the present study in order to provide a context for the analysis of proximal phalanges in the hominin fossil record. To conclude, dorsally reorganized MT head morphologies are recognizable and functionally informative, and this study is the first to quantify these shape characteristics using a 3DGM approach. “Dorsal doming” is a more complex morphology than previously described and involves a combination of several shape changes that together produces the modern human condition.

404

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- Adams, D.C., Otárola-Castillo, E., 2014. Geomorph: an R package for the collection and analysis of geometric morphometric shape data. *Meth. Ecol. Evol.* 4, 393–399.
- Almécija, S., Tallman, M., Alba, D.M., Pina, M., Moyà-Solà, S., Jungers, W.L., 2013. The femur of *Orrorin tugenensis* exhibits morphometric affinities with both Miocene apes and later hominins. *Nat. Commun.* 4, 2888.
- Almécija, S., Orr, C.M., Tocheri, M.W., Patel, B.A., Jungers, W.L., 2015. Exploring phylogenetic and functional signals in complex morphologies: the hamate of extant anthropoids as a test-case study. *Anat. Rec.* 298, 212–229.
- Bates, K.T., Collins, D., Savage, R., McClymont, J., Webster, E., Pataky, T.C., D'Août, K., Sellers, W.I., Bennett, M.R., Crompton, R.H., 2013. The evolution of compliance in the human lateral midfoot. *Proc. Royal Soc. B.* 280, 20131818.
- Bojsen-Møller, F., 1979. Calcaneocuboid joint and stability of the longitudinal arch of the foot at high and low gear push off. *J. Anat.* 129, 165–176.
- Bookstein, F.L., 1997. Morphometric tools for landmark data: geometry and biology. Cambridge University Press, Cambridge.
- Boonratana, R., 2000. Ranging behavior of proboscis monkeys (*Presbytis larvatus*) in the lower Kinabatangan, Northern Borneo. *Int. J. Primatol.* 21, 497–518.
- Cant, J., 1987. Positional behavior of female Bornean orangutans (*Pongo pygmaeus*). *Am. J. Phys. Anthropol.* 12, 71–90.
- Cant, J., 1988. Positional behavior of long-tailed macaques (*Macaca fascicularis*) in Northern Sumatra. *Am. J. Phys. Anthropol.* 76, 29–37.

- Cant, J.G.H., Youlatos, D., Rose, M.D., 2001. Locomotor behavior of *Lagothrix lagothricha* and *Ateles belzebuth* in Yasuni national park, Ecuador: general patterns and nonsuspensory modes. *J. Hum. Evol.* 41, 141–166.
- Congdon, K.A., Ward, C.V., Kimbel, W.H., Johanson, D.C., 2011. The first complete fourth metatarsal of *Australopithecus afarensis* from Hadar, Ethiopia. *Am. J. Phys. Anthropol.* 144, 111.
- DeSilva, J.M., 2008. Vertical climbing adaptations in the anthropoid ankle and midfoot: implications for locomotion in Miocene catarrhines and Plio-Pleistocene hominins. Ph.D. Dissertation, University of Michigan.
- DeSilva, J.M., 2009. Functional morphology of the ankle and the likelihood of climbing in early hominins. *Proc. Nat. Acad. Sci.* 106, 6567–6572.
- DeSilva, J.M., 2010. Revisiting the “midtarsal break”. *Am. J. Phys. Anthropol.* 141, 245–258.
- DeSilva, J.M., Gill, S.V., 2013. Brief communication: a midtarsal (midfoot) break in the human foot. *Am. J. Phys. Anthropol.* 151, 495–499.
- DeSilva, J.M., Proctor, D.J., Zipfel, B., 2012. A complete second metatarsal (StW 89) from Sterkfontein Member 4, South Africa. *J. Hum. Evol.* 63, 487–496.
- DeSilva, J.M., Bonne-Annee, R., Swanson, Z., Gill, C.M., Sobel, M., Uy, J., Gill, S.V., 2015. Midtarsal break variation in modern humans: functional causes, skeletal correlates, and paleontological implications. *Am. J. Phys. Anthropol.* 156, 543–552.
- Doran, D.M., 1992. The ontogeny of chimpanzee and pygmy chimpanzee locomotor behavior: a case study in paedomorphism and its behavioral correlates. *J. Hum. Evol.* 23, 139–157.
- Doran, D.M., 1993. Sex differences in adult chimpanzee positional behavior: the influence of body size on locomotion and posture. *Am. J. Phys. Anthropol.* 91, 99–115.

- Doran, D.M., 1996. Comparative positional behavior of the African apes. In: McGrew, W.C., Marchant, L.F., Nishida, T. (Eds.), *Great Ape Societies*. University Press, Cambridge, pp. 213–224.
- Doran, D.M., 1997. Ontogeny of locomotion in mountain gorillas and chimpanzees. *J. Hum. Evol.* 32, 323–344.
- Doran, D.M., McNeillage, A., 1998. Gorilla ecology and behavior. *Evol. Anthropol.* 6, 120–131.
- Dunbar, R., Dunbar, E., 1974. Ecological relations and niche separation between sympatric terrestrial primates in Ethiopia. *Folia Primatol.* 21, 36–60.
- Dunn, R.H., Tocheri, M.W., Orr, C.M., Jungers, W.L., 2014. Ecological divergence and talar morphology in gorillas. *Am. J. Phys. Anthropol.* 153, 526–541.
- Duncan, A.S., Kappelman, J., Shapiro, L.J., 1994. Metatarsophalangeal joint function and positional behavior in *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 93, 67–81.
- Elftman, H., Manter, J., 1935. The evolution of the human foot, with special reference to the joints. *J. Anat.* 70, 56–67.
- Felsenstein, J., 1985. Phylogenies and the comparative method. *Amer. Nat.* 1, 1–15.
- Fleagle, J.G., 2013. *Primate adaptation and evolution*. Academic Press, San Diego.
- Gomberg, D.N., 1985. Functional differences of three ligaments of the transverse tarsal joint in hominoids. *J. Hum. Evol.* 14, 553–562.
- Gosselin-Ildari, A.D., 2013. The evolution of cercopithecoid locomotion: A morphometric, phylogenetic, and character mapping approach. PhD Dissertation, Stony Brook University.
- Gower, J.C., 1975. Generalized procrustes analysis. *Psychometrika.* 40, 33–51.
- Griffin, N.L., Richmond, B.G., 2010. Joint orientation and function in great ape and human proximal pedal phalanges. *Am. J. Phys. Anthropol.* 141, 116–123.

- Griffin, N.L., D'Août, K., Ryan, T.M., Richmond, B.G., Ketcham, R.A., Postnov, A., 2010a. Comparative forefoot trabecular bone architecture in extant hominids. *J. Hum. Evol.* 59, 202–213.
- Griffin, N.L., D'Août, K., Richmond, B., Gordon, A., Aerts, P., 2010b. Comparative *in vivo* forefoot kinematics of *Homo sapiens* and *Pan paniscus*. *J. Hum. Evol.* 59, 608–619.
- Griffin, N.L., Miller, C.E., Schmitt, D., D'Août, K., 2015. Understanding the evolution of the windlass mechanism of the human foot from comparative anatomy: insights, obstacles, and future directions. *Am. J. Phys. Anthropol.* 156, 1–10.
- Haile-Salassie, Y., Saylor, B.Z., Deino, A., Levin, N.E., Alene, M., Latimer, B.M., 2012. A new hominin foot from Ethiopia shows multiple Pliocene bipedal adaptations. *Nature* 483, 565–569.
- Hayama, S., Chatani, K., Nakatsukasa, M., 1994. The digitigrade hand and terrestrial adaptation in Japanese macaques. *Anthropol. Sci.* 102, 115–125.
- Hamrick, M.W., 1996. Articular size and curvature as determinants of carpal joint mobility and stability in strepsirrhine primates. *J. Morphol.* 230, 113–127.
- Harcourt-Smith, W.E.H., 2002. Form and function in the hominoid tarsal skeleton. Ph.D. Dissertation, University College London.
- Harcourt-Smith, W.E.H., Aiello, L.C., 2004. Fossils, feet and the evolution of human bipedal locomotion. *J. Anat.* 204, 403–416.
- Hicks, J.H., 1954. The mechanics of the foot. II. The plantar aponeurosis and the arch. *J. Anat.* 88, 25–30.
- Holowka, N.B., O'Neill, M.C., Demes, B., 2014. Three-dimensional foot kinematics of chimpanzees and humans during bipedal location. *Am. J. Phys. Anthropol.* 153, 144.

- Jungers, W.L., Burr, D.B., Cole, M.S., 1998. Body size and scaling of long bone geometry, bone strength, and positional behavior in cercopithecoid primates. In: Strasser, E., Fleagle, J.G., Rosenberger, A.L., McHenry, H.M. (Eds.), *Primate Locomotion: Recent advances*. Springer, New York.
- Jungers, W.L., Harcourt-Smith, W.E.H., Wunderlich, R.E., Tocheri, M.W., Larson, S.G., Sutinka, T., Due, R.A., Morwood, M.J., 2009. The foot of *Homo floresiensis*. *Nature* 459, 81–84.
- Jungers, W.L., Grine, F.E., Leakey, M.G., Leakey, L., Brown, F., Yang, D., Tocheri, M.W., 2015. New hominin fossils from Ileret (Kolom Odiet), Kenya. *Am. J. Phys. Anthropol.* 156, 181.
- Kidd, R., 1999. Evolution of the rearfoot. A model of adaptation with evidence from the fossil record. *J. Am. Podiatr. Med. Assoc.* 89, 2–17.
- Klingenberg, C.P., 2011. MorphoJ: an integrated software package for geometric morphometrics. *Mol. Ecol. Resour.* 11, 353–357.
- Knigge, R.P., Tocheri, M.W., Orr, C.M., McNulty, K.P., 2015. Three-dimensional geometric morphometric analysis of talar morphology in extant gorilla taxa from highland and lowland habitats. *Anat. Rec.* 298, 277–290.
- Latimer, B.M., Lovejoy, C.O., 1990. Metatarsophalangeal joints of *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 83, 13–23.
- Latimer, B.M., Ohman, J.C., Lovejoy, C.O., 1987. Talocrural joint in African hominoids—Implications for *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 74, 155–175.
- Lewis, O.J., 1980. The joints of the evolving foot. Part III. The fossil evidence *J. Anat.* 131, 275–298.
- Lewis, O.J., 1989. *Functional morphology of the evolving hand and foot*. Oxford University Press, Oxford.

- Le Minor, J.M., 1988. The ventral metacarpo- and metatarso-phalangeal sesamoid bones: comparative anatomy and evolutionary aspects. *Gegenbaurs Morphol Jahrb* 134, 693–731.
- Lordkipanidze, D., Jashashvili, T., Vekua, A., Ponce de León, M.S., Zollikofer, C.P.E., Rightmire, G.P., Pontzer, H., Ferring, R., Oms, O., Tappen, M., Bukhsianidze, M., Agusti, J., Kahlke, R., Kiladze, G., Martinez-Navarro, B., Mouskhelishvili, A., Nioradze, M., Rook, L., 2007. Postcranial evidence from early *Homo* from Dmanisi, Georgia. *Nature* 449, 305–310.
- Lovejoy, C.O., Latimer, B., Suwa, G., Asfaw, B., White, T.D., 2009. Combining prehension and propulsion: the foot of *Ardipithecus ramidus*. *Science* 326, 72e1–72e8.
- MacConaill, M.A., Basmajian, J.V., 1969. *Muscles and movements*. Williams & Wilkins, Baltimore.
- Meldrum, J.D., 1991. Kinematics of the cercopithecine foot on arboreal and terrestrial substrates with implications for the interpretation of hominid terrestrial adaptations. *Am. J. Phys. Anthropol.* 84, 273–289.
- Morton, D.J., 1922. Evolution of the human foot I. *Am. J. Phys. Anthropol.* 5, 305–336.
- Morton, D.J., 1924. Evolution of the human foot II. *Am. J. Phys. Anthropol.* 7, 1–52.
- Morton, D.J., 1964. *The human foot. Its evolution, physiology and functional disorders*. Hafner Publishing Company, Inc., New York.
- Nakagawa, N., 1989. Activity budget and diet of patas monkeys in Kala Maloue national park: Cameroon: a preliminary report. *Primates* 30, 27–34.
- Nowak, M.G., Carlson, K.J., Patel, B.A., 2010. Apparent density of the primate calcaneo-cuboid joint and its association with locomotor mode, foot posture, and the “midtarsal break”. *Am. J. Phys. Anthropol.* 142, 180–193.

- O'Higgins, P., Jones, N., 1998. Facial growth in *Cercocebus torquatus*: An application of three dimensional geometric morphometric techniques to the study of morphological variation. *J. Anat.* 193, 251–272.
- Patel, B.A., 2010a. Not so fast: speed effects on forelimb kinematics in cercopithecine monkeys and implications for digitigrade postures in primates. *Am. J. Phys. Anthropol.* 140, 92–112.
- Patel, B.A., 2010b. The functional morphology cercopithecoid primate metacarpals. *J. Hum. Evol.* 58, 320–337.
- Patel, B.A., Polk, J.D., 2010. Distal forelimb kinematics in *Erythrocebus patas* and *Papio anubis* during walking and galloping. *Int. J. Primatol.* 31, 191–207.
- Pontzer H., Rolian C., Rightmire, G.P., Jashashvili, T., Ponce de León, M.S., Lordkipanidze, D., Zollikofer, C.P.E., 2010. Locomotor anatomy and biomechanics of the dmanisi hominins. *J. Hum. Evol.* 58, 492–504.
- Preuschoft, H., 1970. Functional anatomy of the lower extremity. In: Bourne, G.H. (Ed.), *The Chimpanzee*, vol. 3. Karger, Basel, pp. 221–294.
- Proctor, D.J., 2010a. Three-dimensional morphometrics of the proximal metatarsal articular surfaces of *Gorilla*, *Pan*, *Hylobates*, and shod and unshod humans. Ph.D. Dissertation, University of Iowa.
- Proctor, D.J., 2010b. Shape analysis of the MT1 proximal articular surface in fossil hominins and shod and unshod *Homo*. *Am. J. Phys. Anthropol.* 143, 631–637.
- Proctor, D.J., 2013. Proximal metatarsal articular surface shape and the evolution of a rigid lateral foot in hominins. *J. Hum. Evol.* 65, 761–769.
- Proctor, D.J., Broadfield, D., Proctor, K., 2008. Quantitative three-dimensional shape analysis of the proximal hallucial metatarsal articular surface in *Homo*, *Pan*, *Gorilla*, and *Hylobates*. *Am. J. Phys. Anthropol.* 135, 216–224.

- Richmond, B.G., Begun, D.R., Strait, D.S., 2001. Origin of human bipedalism: the knuckle-walking hypothesis revisited. *Am. J. Phys. Anthropol.* 116, 70–105.
- Rohlf, F.J., 2010. tpsRelw: relative warps analysis. Version 1.49. Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook.
- Rose, M., 1979. Positional behavior of natural populations: some quantitative results of a field study of *Colobus guereza* and *Cercopithecus atheiops*. In: Morbeck, M.E., Preuschoft, H., Gomberg, N. (Eds.), *Environment, behavior, and morphology: dynamic interactions in primates*. Gustav Fischer, New York.
- Ruff, C., 2008. Femoral/humeral strength in early African *Homo erectus*. *J. Hum. Evol.* 54, 383–390.
- Ruff, C., 2009. Relative limb strength and locomotion in *Homo habilis*. *Am. J. Phys. Anthropol.* 138, 90–100.
- Sarmiento, E.E., 1994. Terrestrial traits in the hands and feet of gorillas. *Am. Mus. Novit.* 3091, 1–56.
- Sarrafian, S.K., 1987. Functional characteristics of the foot and plantar aponeurosis under tibiotalar loading. *Foot Ankle* 8, 4–18.
- Schmitt, D., Larson, S.G., 1995. Heel contact as a function of substrate type and speed in primates. *Am. J. Phys. Anthropol.* 96, 39–50.
- Schultz, A.H., 1930. The skeleton of the trunk and limbs of higher primates. *Hum. Biol.* 2, 303–438.
- Schultz, A.H., 1934. Some distinguishing characters of the mountain gorilla. *J. Mammal.* 15, 51–61.
- Spoor, F., Wood, B., Zonneveld, F., 1994. Implications of early hominid labyrinthine morphology for evolution of human bipedal locomotion. *Nature* 369, 645–648.
- Stern, J.T., 2000. Climbing to the top: A personal memoir of *Australopithecus afarensis*. *Evol. Anthropol.* 9, 111–148.

- Stern, J.T., Susman, R.L., 1983. The locomotor anatomy of *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 60, 279–317.
- Susman, R.L., 1983. Evolution of the human foot: evidence from Plio-Pleistocene hominids. *Foot Ankle* 6, 365–76.
- Susman, R.L., Brain, T.M., 1988. New first metatarsal (SKX 5017) from Swartkrans and the gait of *Paranthropus robustus*. *Am. J. Phys. Anthropol.* 77, 7–15.
- Susman, R.L., de Ruiter, D.J., 2004. New hominin first metatarsal (SK 1813) from Swartkrans. *J. Hum. Evol.* 47, 171–181.
- Susman, R.L., Stern, J.T., 1982. Functional morphology of *Homo habilis*. *Science* 217, 931–934.
- Susman, R.L., Stern, J.T., Jungers, W.L., 1984. Arboreality and bipedality in the Hadar hominids. *Folia Primatol.* 43, 171–181.
- Tocheri, M.W., Solhan, C.R., Orr, C.M., Femiani, J., Frohlich, B., Groves, C.P., Harcourt-Smith, W.E., Richmond, B.G., Shoelson, B., Jungers, W.L., 2011. Ecological divergence and medial cuneiform morphology in gorillas. *J. Hum. Evol.* 60, 171–184.
- Tuttle, R.H., 1970. Postural, propulsive, and prehensile capabilities in the cheiridia of chimpanzees, and other great apes. In: Bourne, G.H. (Ed.), *The chimpanzee*. Karger, Basel, pp. 167–263.
- Vereecke, E., D'Août, K., Clercq, D.D., Elsacker, L.V., Aerts, P., 2003. Dynamic plantar pressure distribution during terrestrial locomotion of bonobos (*Pan paniscus*). *Am. J. Phys. Anthropol.* 120, 373–383.
- Ward, C.V., 2002. Interpreting the posture and locomotion of *Australopithecus afarensis*: where do we stand? *Yearb. Phys. Anthropol.* 35, 185–215.
- Ward, C.V., Kimbel, W.H., Johanson, D.C., 2011. Complete fourth metatarsal and arches in the foot of *Australopithecus afarensis*. *Science* 331, 750–753.

- Ward, C.V., Kimbel, W.H., Harmon, E.H., Johanson, D.C., 2012. New postcranial fossils of *Australopithecus afarensis* from Hadar, Ethiopia (1990–2007). *J. Hum. Evol.* 63, 1–51.
- Wiley, D.F., Amenta, N., Alcantara, D.A., Ghosh, D., Kil, Y.J., Delson, E., Harcourt-Smith, W., Rohlf, F.J., John, K.S., Hamann, B., 2005. Evolutionary morphing [Abstract], IEEE Visualization Conference, Minneapolis, MN, pp. 431–438.
- Wood-Jones, F., 1944. Structure and function as seen in the foot. Bailliere and Co., London.
- Zipfel, B., Kidd, R., 2006. Hominin first metatarsals (SKX 5017 and SK 1813) from Swartkrans: a morphometric analysis. *Homo* 57, 117–131.
- Zipfel, B., DeSilva, J.M., Kidd, R.S., 2009. Earliest complete hominin fifth metatarsal—implications for the evolution of the lateral column of the foot. *Am. J. Phys. Anthropol.* 140, 532–545.
- Zipfel, B., DeSilva, J.M., Kidd, R.S., Carlson, K.J., Churchill, S.E., Berger, L.R., 2011. The foot and ankle of *Australopithecus sediba*. *Science* 333, 1470–1420.

Figure legends

Figure 1. Comparative morphology of catarrhine right first metatarsals (MTs). Apes are characterized by highly curved MT shafts terminating in a strong plantar orientation of the MT head and narrow, rounded MT heads (arrows); monkeys and humans have straight MTs terminating in a more dorsally oriented MT head (arrow). Note that *Homo* is characterized by dorsal overlap of the distal articular surface onto the MT shaft and by wide flattening of the dorsal articular surface (arrows). Left column: lateral view. Right column: distal view. Bar: 1 cm.

Figure 2. 3D landmark surface patch boundaries. A *Homo sapiens* right MT1 head with a 5x5 landmark patch applied to the distal articular surface is presented in multiple views. Red rectangles = landmarks, black rectangles = semi-landmarks, solid lines = approximate surface patch boundaries and patch grid connecting landmarks/semi-landmarks. Landmark locations are approximate. Semi-landmarks are placed automatically between landmark positions and are evenly spaced using standardized sliding algorithms (e.g., minimized Procrustes distance and minimized bending energy criteria).

Figure 3. PCA scatterplots of PC1 vs. PC2 for repeated measures. Circles = individuals, rectangles = repeated measures. The relative clustering of repeated measures demonstrates that the landmarks chosen are very repeatable. a) *Homo sapiens* MT1, b) *Pongo pygmaeus* MT4, c) *Papio ursinus* MT2, d) *Gorilla* sp. MT3. *Hylobates* sp. MT5 not shown, but results are very similar to these repeatability scatterplots.

Figure 4. PCA scatterplot of PC1 vs. PC2 for MT1. Note the general separation of apes, monkeys, and humans. PC1 strongly tracks dorso-plantar orientation of the MT head and plantar

condylar morphology, whereas PC2 tracks MT1 head width. Wireframes and 3D surface morphs represent articular shape differences of observed extremes (PC1: -0.15–0.15; PC2: -0.08–0.12).

Figure 5. Box-and-whisker plots of PC1 and PC2 for the MT1. Wireframes and 3D surface morphs represent articular shape differences of observed extremes. Generally, humans overlap with cercopithecoids in PC1 (dorso-plantar head orientation) and apes in PC2 (MT1 head width). In PC1, the top morphs are shown in distal view and the bottom morphs are shown in lateral view. In PC2, the top morphs are shown in lateral view and the bottom morphs are shown in distal view. Shaded blue bar = human range, vertical bars = median, rectangles = interquartile range, horizontal bars = range.

Figure 6. PCA scatterplot of PC1 vs. PC2 for MT2. Note the general separation of apes, monkeys, and humans, with humans separating far along PC2 from all taxa. PC1 primarily tracks MT head orientation and PC2 primarily tracks dorsal widening of the MT head, characteristic of modern humans. Wireframes represent articular shape differences of observed extremes (PC1: -0.12–0.15; PC2: -0.08–0.12).

Figure 7. Box-and-whisker plots of PC1 and PC2 for the MT2. Wireframes and 3D surface morphs represent articular shape differences of observed extremes. Note the far separation of *Homo* compared to other catarrhines in PC2. In PC1, the top morphs are shown in lateral view and the bottom morphs are shown in distal view. In PC2, the top morphs are shown in lateral view and the bottom morphs are shown in distal view. Shaded blue bar = human range, vertical bars = median, rectangles = interquartile range, horizontal bars = range.

Table 1. Sample sizes for extant taxa

Taxon	Locomotor mode^a	Foot posture^b	μCT	CT	Laser scan
<u>Hominoids</u>					
<i>Homo sapiens</i>	B	FCP	-	22	-
<i>Gorilla beringei beringei</i>	KW/C	IHSP	-	3	3
<i>Gorilla beringei graueri</i>	KW/C	IHSP	-	3	-
<i>Gorilla gorilla gorilla</i>	KW/C	IHSP	-	4	4
<i>Pan troglodytes</i>	KW/C	IHSP	-	6	10
<i>Pongo pygmaeus</i>	S	IHSP	-	-	10
<i>Hylobates lar</i>	R	MFP	10	-	-
<u>Cercopithecoids</u>					
<i>Papio ursinus</i>	TQ	DG/SP	10	-	-
<i>Macaca nemestrina</i> ³	TQ	DG/SP	9	-	-
<i>Macaca fascicularis</i> ³	AQ	DG/SP	7	-	-
<i>Nasalis larvatus</i> ³	AQ	DG/SP	10	-	-

^a B = biped, KW/C = knuckle-walking/climber, S = suspensory/quadrumanous climber, R = ricochet brachiator, TQ = terrestrial quadruped, AQ = arboreal quadruped

^b FCP = full contact plantigrade, IHSP = inverted heel-strike plantigrade, MFP = midfoot plantigrade, DG/SP = digitigrade/semiplantigrade. Foot postures and general locomotor categories were determined based on descriptions in the literature (Dunbar and Dunbar, 1974; Rose, 1979; Nakagawa, 1989; Doran, 1992, 1993; Schmitt and Larson, 1995; Cant, 1987, 1988; Jungers et al., 1998; Boonratana, 2000; Cant et al., 2001; Vereecke et al., 2003; Nowak et al., 2010; Fleagle, 2013; Gosselin-Ildari, 2013).

Table 2. List of landmarks on each metatarsal (MT) head^a

Landmark number	Type	Landmark description
1	Type II	Most medially protruding point on medial epicondyle
2	Type III	Midpoint between point 1 and 3, medial ridge separating distal articular surface from MT diaphysis
3	Type II	Most plantarly projecting point on medial plantar condyle
4	Type II	Dorsal most point on dorsal surface of MT articular surface
5	Type II	Most distally projecting point on MT head
6	Type III	Most plantarly projecting point on intercondylar ridge
7	Type II	Most laterally protruding point on lateral epicondyle
8	Type III	Midpoint between point 7 and 9, lateral ridge separating distal articular surface from MT diaphysis
9	Type II	Most plantarly projecting point on lateral plantar condyle

^aSemilandmark locations are calculated using minimized Procrustes distance between reference landmarks, please refer to Figure 2 for semilandmark location placement on the distal MT articular surface.

Table 3. Percent total variance explained by each principle component (PC) on 3D metatarsal (MT) shape data accounting for at least 5% of the total variance^a

PC	MT1	MT2	MT3	MT4	MT5
1	26	27	33	28	27
2	11	15	13	16	16
3	10	8	9	10	10
4	9	7	8	8	8
5	5	5	5	6	5

^aPC1 and PC2 captured the most relevant shape changes related to dorsal MT head morphology.

Table 4. Post-hoc Tukey's HSD results on PC1 comparing genera following a MANOVA on MT1 shape variables (PC1–PC5)^a

Genus	<i>Nasalis</i>	<i>Macaca</i>	<i>Papio</i>	<i>Hylobates</i>	<i>Pongo</i>	<i>Gorilla</i>	<i>Pan</i>	<i>Homo</i>
<i>Nasalis</i>	1.0000	-	-	-	-	-	-	
<i>Macaca</i>	0.0479	1.0000	-	-	-	-	-	-
<i>Papio</i>	0.6760	1.0000	1.0000	-	-	-	-	-
<i>Hylobates</i>	<0.0001	0.0554	0.0401	1.0000	-	-	-	-
<i>Pongo</i>	<0.0001	<0.0001	<0.0001	<0.0001	1.0000	-	-	-
<i>Gorilla</i>	<0.0001	<0.0001	<0.0001	0.0012	0.3929	1.0000	-	-
<i>Pan</i>	<0.0001	<0.0001	<0.0001	0.2641	0.0091	0.5770	1.0000	-
<i>Homo</i>	0.4739	0.4590	0.7328	<0.0001	<0.0001	<0.0001	<0.0001	1.0000

^aPC1 tracked MT head orientation, epicondylar breadth, and plantar condylar morphology. *Homo* and cercopithecoids overlap on PC1 to the exclusion of apes. Values of significance at $\alpha = 0.05$ are in bold.

Table 5. Post-hoc Tukey's HSD results on PC2 comparing genera following a MANOVA on MT1 shape variables (PC1–PC5)^a

Genus	<i>Nasalis</i>	<i>Macaca</i>	<i>Papio</i>	<i>Hylobates</i>	<i>Pongo</i>	<i>Gorilla</i>	<i>Pan</i>	<i>Homo</i>
<i>Nasalis</i>	1.0000	-	-	-	-	-	-	
<i>Macaca</i>	0.0275	1.0000	-	-	-	-	-	-
<i>Papio</i>	0.0536	1.0000	1.0000	-	-	-	-	-
<i>Hylobates</i>	1.0000	0.0721	0.1214	1.0000	-	-	-	-
<i>Pongo</i>	0.3357	<0.0001	<0.0001	0.2416	1.0000	-	-	-
<i>Gorilla</i>	0.8965	<0.0001	<0.0001	0.7911	0.9417	1.0000	-	-
<i>Pan</i>	0.0396	1.0000	1.0000	0.0933	<0.0001	<0.0001	1.0000	-
<i>Homo</i>	0.0118	<0.0001	<0.0001	0.0077	0.9373	0.1865	<0.0001	1.0000

^aPC2 corresponds to overall mediolateral breadth of the MT head but also drives dorsal MT head orientation, although to a lesser extent than seen in PC1. Humans overlap with gorillas and orangutans, which are both characterized by wide MT heads, and separate from cercopithecoids, gibbons, and chimpanzees, which are characterized by more narrow, rounded MT heads. Values of significance at $\alpha = 0.05$ are in bold.

Table 6. Post-hoc Tukey's HSD results on PC1 comparing genera following a MANOVA on MT2 shape variables (PC1–PC5)^a

Genus	<i>Nasalis</i>	<i>Macaca</i>	<i>Papio</i>	<i>Hylobates</i>	<i>Pongo</i>	<i>Gorilla</i>	<i>Pan</i>	<i>Homo</i>
<i>Nasalis</i>	1.0000	-	-	-	-	-	-	
<i>Macaca</i>	0.0217	1.0000	-	-	-	-	-	-
<i>Papio</i>	<0.0001	<0.0001	1.0000	-	-	-	-	-
<i>Hylobates</i>	<0.0001	<0.0001	<0.0001	1.0000	-	-	-	-
<i>Pongo</i>	<0.0001	<0.0001	<0.0001	0.9900	1.0000	-	-	-
<i>Gorilla</i>	<0.0001	<0.0001	<0.0001	0.4431	0.9532	1.0000	-	-
<i>Pan</i>	<0.0001	<0.0001	<0.0001	0.8713	0.3783	0.0169	1.0000	-
<i>Homo</i>	0.4581	<0.0001	<0.0001	<0.0001	0.0013	0.0081	<0.0001	1.0000

^aPC1 corresponds to dorsal orientation of the MT head, as well as width of the mediolateral MT head articular margin. Humans separate from all taxa except *Nasalis*, which has similar mediolateral articular margin width as seen in *Homo*. *Hylobates* was marked by high variability on PC1 in the lateral MTs and only separated from humans. Values of significance at $\alpha = 0.05$ are in bold.

Table 7. Post-hoc Tukey's HSD results on PC2 comparing genera following a MANOVA on MT2 shape variables (PC1–PC5)^a

Genus	<i>Nasalis</i>	<i>Macaca</i>	<i>Papio</i>	<i>Hylobates</i>	<i>Pongo</i>	<i>Gorilla</i>	<i>Pan</i>	<i>Homo</i>
<i>Nasalis</i>	1.0000	-	-	-	-	-	-	
<i>Macaca</i>	<0.0001	1.0000	-	-	-	-	-	-
<i>Papio</i>	0.3052	0.0292	1.0000	-	-	-	-	-
<i>Hylobates</i>	0.0329	0.2555	0.9860	1.0000	-	-	-	-
<i>Pongo</i>	<0.0001	0.9227	0.0044	0.0426	1.0000	-	-	-
<i>Gorilla</i>	0.7828	<0.0001	0.9812	0.5238	<0.0001	1.0000	-	-
<i>Pan</i>	0.1273	0.0654	1.0000	0.9990	0.0091	0.0874	1.0000	-
<i>Homo</i>	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	1.0000

^aPC2 corresponds to dorsal mediolateral breadth of the MT head. *Homo* separates significantly from all other genera on this axis, whereas the other genera largely overlap. Values of significance at $\alpha = 0.05$ are in bold.

Table 8. Proportion of explained variance for several multivariate regressions of shape data on size and phylogenetic variables^a

	% Shape predicted				
	MT1	MT2	MT3	MT4	MT5
Catarrhines + Size	14.6	4.6	13.6	11.0	22.6
Catarrhines + Size (PICS)	7.1	5.9	8.7	9.25	9.8
Catarrhines + Species	22.1	29.9	36.9	8.4	30.1

^aResults suggest that size was not a significant predictor of shape.

PICS = Phylogenetic Independent Contrasts. Size = log centroid size.

Figure 1

Figure 2

Distal

Dorsal

Lateral

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7